# Changes in serum androgens and estrogens during spawning in bluefish, *Pomatomus saltator*, and king mackerel, *Scomberomorus cavalla*[1]

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Androgens and estrogens were assayed by radioimmunoassay (RIA) technique in serum of bluefish, *Pomatomus saltator*, and king mackerel, *Scomberomorus cavalla*. Both species were collected in the northeast Gulf of Mexico from August through November 1979. When categorized by stage of ovarian development a significant correlation between gonadosomatic indices (GSI) and serum estrogens was observed among female *S. cavalla* but not among *P. saltator*. Among males and females of both species, a significant correlation between GSI and serum androgens occurred. Peak levels of androgens in male king mackerel (38.12 ± 11.21 ng/mL) were not significantly different from peak levels of females (33.14 ± 5.10 ng/mL). However, in female bluefish, androgens peaked at 3.68 ± 0.88 ng/mL, twofold greater than in males (1.66 ± 0.28 ng/mL). Following this peak, a significant reduction in androgens occurred in ripe female bluefish. No significant change in estrogens occurred in these females. Although the functional significance of changes in androgens in spawning female bluefish was not determined, serum androgen levels may be a useful tool in identifying and timing maturation and spawning in both male and female teleosts.

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Une technique radioimmunologique (RIA) a permis d'analyser les androgènes et les oestrogènes du sérum chez le tassergal *Pomatomus saltator* et le scombre *Scomberomorus cavalla*. Les deux espèces ont été capturées dans la portion nord-est du Golfe du Mexique, d'août à la fin de novembre 1979. La classification en fonction du développement ovarien révèle qu'il existe une corrélation significative entre l'indice gonadosomatique (GSI) et les oestrogènes sériques chez les femelles de *S. cavalla*, mais pas chez les femelles de *P. saltator*. Il existe une corrélation significative entre l'indice gonadosomatique (GSI) et les androgèns sériques chez les mâles et les femelles dex deux espèces. Chez le scombre, les concentrations maximales d'androgènes des mâles (38,12 ± 11,21 ng/mL) ne sont pas significativement différentes de celles des femelles (33,14 ± 5,10 ng/mL). Cependant, chez les femelles du tassergal, les concentrations d'androgèns maximales (3,68 ± 0,88 ng/mL) sont deux fois plus élevées que les concentrations maximales des mâles (1,66 ± 0,28 ng/mL). Après cela, il se produit une importante diminution des androgènes chez les femelles à maturité. Les concentrations d'oestrogènes changent peu chez ces femelles. L'importance fonctionnelle des changements de concentration d'androgènes pendant la période de la fraye, chez les femelles du tassergal, n'a pas été déterminée, mais les concentrations d'androgènes du sérum peuvent très bien servir à déterminer le moment de la maturation et celui de la fraye chez les mâles et les femelles de téléostéens.

[Traduit par le journal]

## Introduction

Several studies of seasonal endocrine changes in teleost fishes have reported variations in blood steroid levels in association with developmental changes of gonads. Concomitant with gonadal maturation, changes in plasma estrogens and androgens have been shown in *Salmo salar* (Idler *et al.* 1971), *Salmo gairdneri* (Lambert *et al.* 1978), *Salmo trutta* (Crim and Idler 1978), *Pleuronectes platessa* (Wingfield and Grimm 1977), *Pseudopleuronectes americanus* (Campbell *et al.* 1976), and *Mugil cephalus* (Dindo and MacGregor 1981). These variations in circulating gonadal steroids may be indicators of stages of reproductive development in teleost fishes.

Two important sport and commercial fishes of the Atlantic and Gulf of Mexico are bluefish, *Pomatomus saltator* (Pomatomidae), and king mackerel, *Scomberomorus cavalla* (Scombridae). Spawning of bluefish in the Atlantic occurs in all seasons of the year, but principally during the spring and summer months (Wilk 1977; Kendall and Walford 1979). In the Gulf of Mexico fall spawning of bluefish is inferred from larval collections off the Texas coast (Barger *et al.* 1978) and from

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gonadal analyses off the northwest Florida coast (Finucane *et al.* 1980). King mackerel spawn from late spring through the summer off the northeast gulf coast (J. H. Finucane, L. A. Collins, H. A. Brusher, and C. H. Saloman, unpublished data[2]) and along the Atlantic coast (Beaumariage 1973). Although spawning is documented for these two marine species, very little is known about their seasonal reproductive development. With the aid of the radioimmunoassay (RIA) technique, measurements of circulating levels of gonadal steroids can be associated with specific stages of reproductive development. The purposes of the present study were to determine whether serum estrogens and androgens would reflect seasonal reproductive development, and to correlate changes in steroid levels with the time of spawning in female and male bluefish and king mackerel.

## Materials and Methods

Fifty-nine female and 33 male bluefish and 40 female and 23 male king mackerel were obtained from recreational and gill net fishermen in bay and gulf waters near Panama City, Florida, from August through November, 1979. Live, fresh-caught fish were kept on ice for 2 to 4 h until blood and gonads were removed. To assess the effects of length of time between capture and blood collection, several fish were sampled immediately after capture for comparison with fish held on ice. Fish were weighed to the nearest gram and gonads to the nearest 0.1 g. The gonadosomatic index (GSI) was computed by dividing the fresh weight of the gonad by the total body weight. Gonads were preserved in 10% formalin. Microscopic examination of oocytes was made to determine the developmental stage of ovaries according to the following description from Finucane *et al.* (1980). The stages were (I) immature, gonads elongate, slender, ova not visible to naked eye, ova mostly transparent oogonia, and primary oocytes with opaque center (diameter: 0.02–0.20 mm); (II) early maturing, gonads slightly enlarged, most ova not visible to naked eye, ova similar to stage I with a few larger (0.10–0.30 mm) fully opaque oocytes; (III) late maturing, gonads enlarged and turgid, many ova visible to naked eye, large fully opaque oocytes predominate (0.30–0.60 mm) with few hydrated, transparent, mature oocytes; (IV) ripe, gonads greatly enlarged from stage III, many clear, hydrated ova visible to naked eye (0.60–1.00 mm), very prominent and easily dislodged from follicles or loose in lumen of ovary; (V) spawned or spent, gonads flaccid with large ova in various stages of resorption (0.40–1.00 mm) and many small stage I and II oocytes. The average GSI for each stage of these fish is given in Table 2.

Blood was obtained from the dorsal aorta, placed into a glass centrifuge tube, and stored on ice for several hours. Serum was separated from coagulated blood after centrifugation (500 g) for 15 min and stored at −20°C until steroids were analyzed.

[2]Reproduction of king mackerel, *Scomberomorus cavalla*, from the southeastern United States during 1977 and 1978. Unpublished manuscript.

*Serum radioimmunoassays*

The antiserum for estrogen assay was purchased from New England Nuclear (Boston, MA). This antiserum, as determined by the manufacturer, has significant crossreaction, relative to 17β-estradiol (100%), with estrone (50%), 17α-estradiol (25%), and estriol (5%).

The antiserum to testosterone (New England Nuclear), as determined by the authors, has relative crossreaction to other steroids as follows: dihydrotestosterone (DHT), 56%; 11-ketotestosterone (11-KT) and 11β-hydroxytestosterone (11-HT), 16%; estradiol and progesterone, less than 0.1%. Although testosterone has been identified in many male and female teleosts (Ozon 1972), 11-KT has been confirmed in only a few marine teleosts (Idler *et al.* 1971; Katz and Eckstein 1974). Serum from both male and female fish were extracted and assayed for androgens and serum from females for estrogens by a modification of the radioimmunoassay (RIA) procedures described by Auletta *et al.* (1974) and Orczyk *et al.* (1974).

*RIA protocol*

Androgens were extracted from duplicate 100 μL aliquots of serum with 1.0 mL of nanograde petroleum ether: benzene (5:2 v/v) followed by vortex mixing for 1 min. The phases were allowed to separate, tubes were snap frozen, and the organic phase decanted into 10 × 75 mm glass tubes. The serum extraction was repeated once and the organic phases were combined for each sample. The organic phase was dried under air at 40°C in preparation for the RIA procedure.

Estrogens were extracted with 1.0 mL of anesthetic grade ether added to duplicate 100-μL aliquots of serum. The extraction procedure was the same as for androgen extraction.

The dried sample residue was redissolved in 100 μL of assay buffer (pH 7.4, 0.1 *M* phosphate, 0.1% sodium azide, 0.5% bovine serum albumin; 0.1% bovine gamma globulin was added for estrogen assays). Assay buffer (100 μL) containing 15 000 DPM of [$^3$H]testosterone or [$^3$H]17β-estradiol (tracer) was added to the petroleum ether or anesthetic ether extract residues, respectively. Antisera to testosterone or estrogen was diluted in assay buffer such that 40–50% of [$^3$H]testosterone or 17β-estradiol was bound in the absence of additional steroids (sample residue or standards). Diluted antiserum (100 μL) was added and the tubes were incubated for 12–18 h at 4°C. Standard curves were determined after adding 100 μL of serially diluted steroids (2000, 1000, 500, 250, 100, 50, 25, 10, 5, and 0 pg/100 μL) in assay buffer to duplicate tubes with antisera and appropriate tracer. Blanks (NSB) containing only tritiated steroid in 300 μL of assay buffer also were prepared. Reagent blanks were prepared by solvent extraction of assay buffer, the residue then was incubated with appropriate tracer and antiserum. Standards and blanks were incubated simultaneously with serum samples. Dextran–charcoal solution (1.0 mL) was added to separate bound from free steroids by centrifugation at 1000 *g* for 15 min at 4°C. Supernatant (bound fraction) was decanted into 10 mL of xylene-based liquid scintillation cocktail (ACS, Amersham) and counted for 5 min in a Beckman LS7000. Standards and samples were compared on a standard curve as percentage of zero standard binding (zero = 100%).

*Criteria for assay*

Triplicate 100-μL aliquots of pooled male or female serum with 1000 cpm of [$^3$H]testosterone (10 pg) or [$^3$H]17β-estradiol (12 pg) were extracted and assayed to determine extraction efficiency for sample correction and assay variability. Recovery of testosterone from petroleum ether extraction was 85 ± 3% (SD); recovery for estradiol from anesthetic ether extraction was 75 ± 5% (SD). Intraassay coefficient of variance (CV) was 9.2% for androgens and 8.6% for estrogens. The interassay CV was 19.9% for androgens and 16.5% for estrogens. Reagent blanks read 10 ± 5 pg (SD) for androgens and 15 ± 7 pg (SD) for estrogens. Therefore aliquots reading less than 15 pg/100μL (androgen) or 20 pg/100μL (estrogen) were considered nondetectable. Only one group of serum samples contained less than 15 pg/100 μL of androgen. These were rerun using 200 μL of serum. Accuracy of the assays with serum from either bluefish or king mackerel was determined by measurements of aliquots of different volumes (10, 25, 50, 100, and 200 μL) of the same pool to demonstrate a linear response, i.e. 50 μL of serum was found to contain half as much steroid as 100 μL of serum. The data were tested for significant differences by a multivariate analysis of variance with orthogonal comparisons (Barr *et al.* 1979).

## Results

To assess the effects of variable lengths of time between capture and blood sample collection on steroid concentrations two groups of bluefish were collected by hook and line during a 4-h period. Group 1 was placed on ice after capture and blood samples were collected at the end of the capture period. Group 2 was sampled with a syringe from the caudal vein immediately after capture. The data (Table 1) indicate that the length of time between capture and blood collection had no significant effect on the values of serum androgens and estrogens.

Data from serum estrogen and androgen and gonadosomatic indices (GSI) of female bluefish and king mackerel were categorized by stages of oocyte development (Table 2). Serum androgen and GSI were determined to be significantly correlated in female bluefish ($r = 0.605$, $P < 0.001$) and female king mackerel ($r = 0.95$, $P < 0.01$). Although a similar positive correlation between serum estrogen and GSI ($r = 0.98$, $P < 0.01$) was found in female king mackerel, no significant correlation between estrogen and GSI occurred in female bluefish. Serum androgen and GSI reached a peak at stage IV (androgen: 1.70 ± 0.41 ng/mL; GSI: 5.30 ± 0.61% body weight) in bluefish and at stage III (androgen: 33.14 ± 5.10 ng/mL; GSI: 2.10 ± 0.30%) in king mackerel. No ripe (stage IV) female king mackerel were collected during this study.

Among female bluefish, ripe (stage IV) females were predominate from late September through late October (Fig. 1). Serum androgen varied significantly during this

TABLE 1. Serum steroid concentrations and gonadosomatic indices (GSI) of female bluefish sampled after fish were held on ice for 2 to 4 h (group 1) or immediately after capture (group 2)

| | | Serum | | |
|---|---|---|---|---|
| | | Androgens, ng/mL | Estrogens, ng/mL | GSI, % body weight |
| Group 1 | 13 | 3.99±0.57[a] | 1.23±0.16 | 5.94±0.38 |
| Group 2 | 17 | 4.09±0.54 | 1.35±0.18 | 5.25±0.35 |

[a]Mean ± standard error.

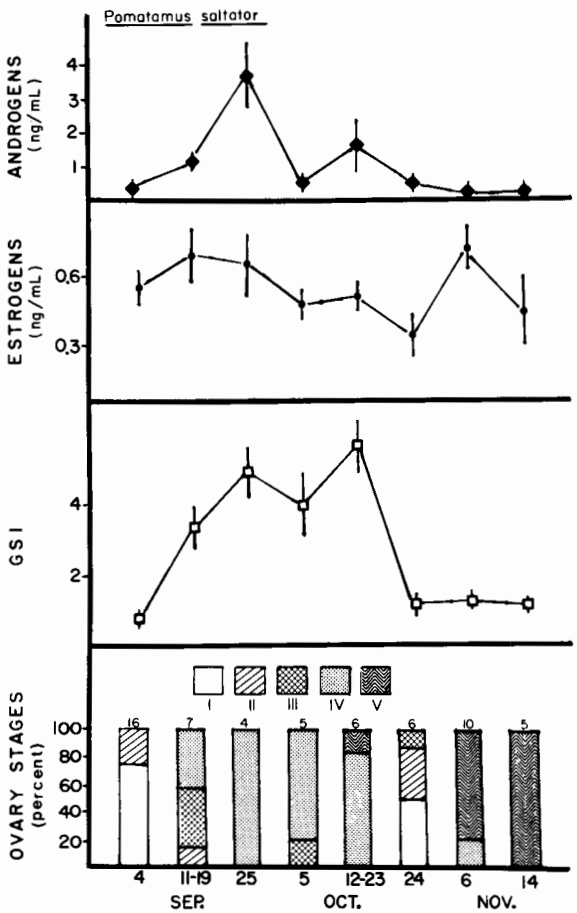


FIG. 1. Serum androgens and estrogens, gonadosomatic indices (GSI), and ovarian development states (percent) in female bluefish (*Pomatomus saltator*) from August through November, 1979, collected in the northeast Gulf of Mexico. Numbers above bars are number of animals per date. Point values from date are mean ± standard error.

TABLE 2. Serum steroid concentrations and gonadosomatic indices (GSI) of female bluefish (*P. saltator*) and king mackerel (*S. cavalla*) at various stages of ovarian development

| | Oocyte stages | | | | |
|---|---|---|---|---|---|
| | I | II | III | IV | V |
| Bluefish | | | | | |
| *N*[a] | 14 | 7 | 5 | 18 | 4 |
| Estrogens, ng/mL | 0.44±0.07[b] | 0.73±0.13 | 0.69±0.11 | 0.60±0.05 | 0.67±0.08 |
| Androgens, ng/mL | 0.38±0.09 | 0.49±0.13 | 0.73±0.27 | 1.70±0.41 | 0.14±0.03 |
| GSI, % | 0.67±0.04 | 1.21±0.18 | 3.25±0.49 | 5.30±0.61 | 0.98±0.08 |
| King mackerel | | | | | |
| *N* | 9 | 10 | 10 | 0 | 11 |
| Estrogens, ng/mL | 0.75±0.24 | 2.40±0.83 | 3.48±0.67 | — | 0.34±0.06 |
| Androgens, ng/mL | 4.90±1.43 | 26.16±6.48 | 33.14±5.10 | — | 1.29±0.30 |
| GSI, % | 0.62±0.07 | 1.31±0.16 | 2.10±0.30 | — | 0.61±0.04 |

[a]Number of samples assayed for each group.
[b]Mean ± standard error.

spawning period. In females collected on September 25 (stage IV; GSI: 4.95 ± 0.70%), androgens (3.68 ± 0.88 ng/mL) were threefold greater ($P < 0.01$) than in females (stages II–IV; GSI: 3.38 ± 0.60%) collected 1 week earlier. However, in ripe females (stage IV; GSI: 4.02 ± 0.92%) collected 2 weeks later (October 2–5) androgens (0.52 ± 0.12 ng/mL) were 86% less than the previous level ($P < 0.01$). An apparent rise in androgens in females collected from October 12 through 23 reflected the average of two high-level females (4.00 ± 0.12 ng/mL) and three low-level females (0.55 ± 0.07 ng/mL). Estrogens did not significantly change in female bluefish from September through November. An apparent rise in estrogen levels on November 6 was not different from levels in fish from any other date, except October 24 ($P < 0.05$). The low levels of estrogens on October 24 reflected a greater frequency (50%) of immature (stage I) females compared with earlier collections in October.

Bluefish males became sexually mature prior to females (Figs. 1 and 2). Gonadosomatic indices rose rapidly in September, reached a peak on September 19 (3.30 ± 0.56% body weight), and coincident with those of females, were significantly lower ($P < 0.1$) in the postspawning period of November (0.54 ± 0.11). Serum androgen showed a similar pattern to GSI, rapidly reaching a peak of 1.66 ± 0.28 ng/mL on September 19. However, androgens had begun to fall by mid-October, reaching their lowest levels in early November (0.18 ± 0.02 ng/mL).

Among female king mackerel, most ovaries contained early and late developing oocytes (stages II and III) during August and September, and fish with ovaries of spent condition (stage V) occurred in late September through October (Fig. 3). No ripe females were obtained during this study. Serum androgen (32.33 ± 3.16 ng/mL) and estrogen (3.85 ± 0.68 ng/mL) were highest

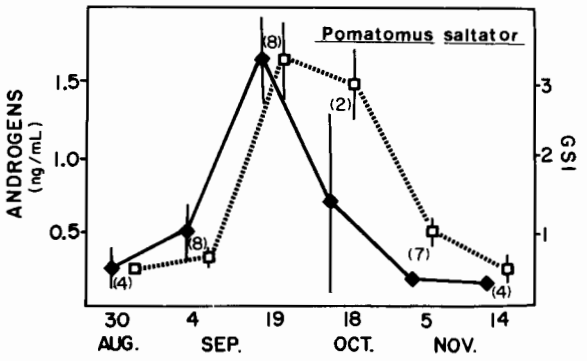


FIG. 2. Serum androgens and gonadosomatic indices (GSI) in male bluefish from August through November, 1979. Each point is the mean ± standard error. Numbers in parentheses refer to number of animals per date. GSIs are represented by open squares.

in August ($P < 0.01$) compared with their lowest levels in October (androgen 0.89 ± 0.42 ng/mL); estrogen: 0.48 ± 0.04 ng/mL). The gonadosomatic indices also were higher in August (1.66 ± 0.32% body weight; $P < 0.05$) than in October (0.61 ± 0.04%).

King mackerel males presented a pattern of declining GSIs and serum testosterone similar to that observed in females (Fig. 4). Although a rapid fall in GSI occurred in August, serum androgen gradually declined from a peak (38.13 ± 11.21 ng/mL) in August to their lowest levels in October (6.78 ± 1.66 ng/mL).

## Discussion

Our results demonstrate that serum androgen levels were significantly correlated with the gonadosomatic indices (GSI) in females and males of both bluefish and king mackerel. Only in female king mackerel did a significant correlation between GSI and serum estrogen occur. These correlations would suggest that of the two

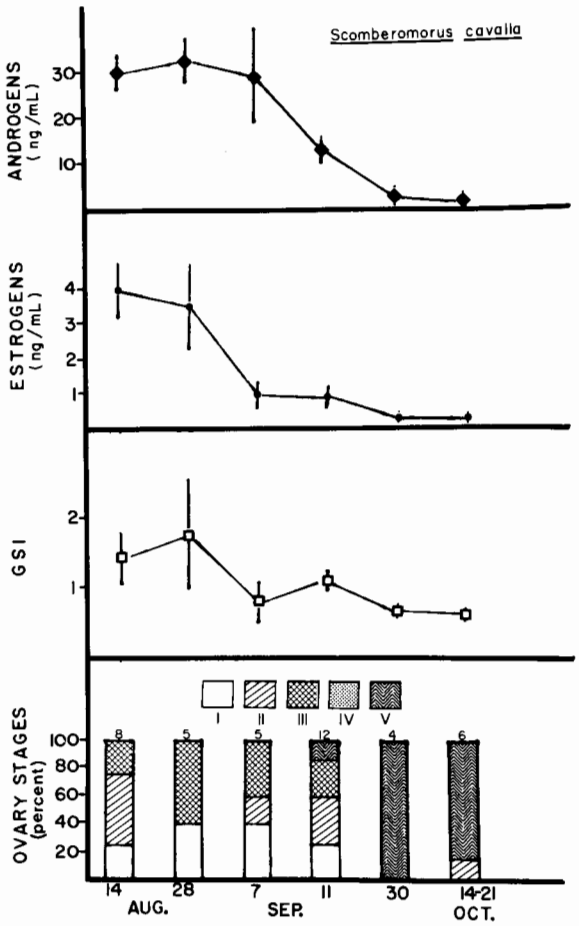


FIG. 3. Serum androgens and estrogens, gonadosomatic indices (GSI), and ovarian development states (percent) in female king mackerel (*Scomberomous cavalla*) from August through October, 1979, collected from the northeast Gulf of Mexico. Numbers above bars are number of animals per date. Point values for each data are mean ± standard error.

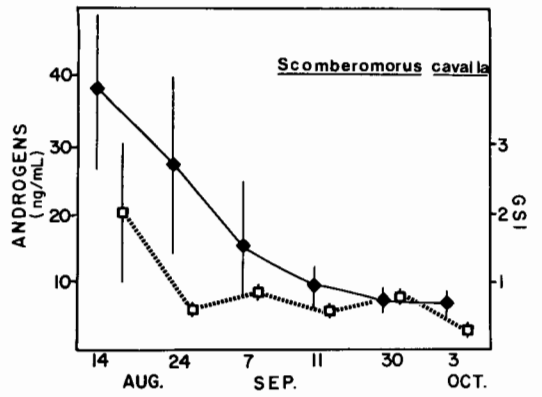


FIG. 4. Serum androgens and gonadosomatic indices (GSI) in male king mackerel from August through October, 1979. Each point is the mean ± standard error. Numbers in parentheses refer to the number of animals per date. GSIs are represented by open squares.

classes of serum steroids, androgens provide a reliable indication of the gonadal condition in both species.

The observed changes in serum androgen and estrogen levels concomitant with ovarian development in the king mackerel are in agreement with studies on winter flounder, *Pseudopleuronectes americanus* (Campbell *et al.* 1976), and plaice, *Pleuronectes platessa* (Wingfield and Grimm 1977). Estrogens are known to be involved principally in liver stimulation of vitellogenesis in both teleosts and amphibians (Campbell and Idler 1976; Schuetz 1974; Tata 1978). Wingfield and Grimm (1977) suggested that testosterone was present in the blood primarily as a precursor to estrogen synthesis. In plaice, estradiol levels were greater than testosterone in females. However, serum androgen in female king mackerel was 10-fold greater than estrogen in the same females and not different from levels in males. Additionally, in bluefish, the rise and fall of serum androgen observed in ripe females was not paralleled by a change in serum estrogens (Fig. 1). These results suggest that there are biological functions for testosterone in these maturing female teleosts other than as precursors to estrogens.

Lance and Callard (1978) had suggested from reports of exceptionally high levels of testosterone in female teleosts that further research was needed. Large increases in testosterone and 11-ketotestosterone were observed in the blood and ovaries of prespawning (mature) as compared with postspawning *Tilapia aurea*, whereas no estrogens were detected (Katz and Eckstein 1974). Also *in vitro* production of androgens in prespawned ovaries was significantly greater than in postspawned ovaries of *Tilapia aurea* (Eckstein and Katz 1971) and *Sparus aurata* (Eckstein *et al.* 1978). These authors did not suggest a specific function for testosterone or other androgens in the maturing female teleost. The fluctuations in serum androgens observed in ripe female bluefish suggest several potential roles. The high levels of androgens may directly stimulate oocyte maturation. Testosterone, which binds to receptors in the cortical layer of oocytes, caused germinal vesicle breakdown, *in vitro*, in oocytes of *Oryzias latipes* (Iwamatsu 1978) and several amphibians (Brachet 1978). Alternatively, these serum androgens may reflect a gonad–pituitary negative feedback system by which the fluctuation in serum androgen instead of estrogen brings about an increase in gonadotropin secretion to stimulate the process of maturation and ovulation (Fontaine 1976; Jalabert 1976).

In males, androgens may stimulate the later stage of spermatogenesis. Highest levels of serum androgen occurred concurrent with maximal GSIs in both bluefish (Fig. 2) and king mackerel (Fig. 4). This is consistent

with changes in circulating levels of androgens in Atlantic salmon, *Salmo salar* (Idler *et al.* 1971), sockeye salmon, *Oncorhynchus nerka* (Schmidt and Idler 1962), plaice, *Pleuronectes platessa* (Wingfield and Grimm 1977), and winter flounder, *Pseudopleuronectes americanus* (Campbell *et al.* 1976).

In summary, the results of the present study indicate that changes in serum androgen are significantly correlated with the gonadal condition of both sexes of bluefish and king mackerel. This correlation is paralleled by serum estrogens in female king mackerel but the absence of fluctuations in estrogens in bluefish is yet unexplained. In bluefish, changes in serum androgen levels may indicate the time of spawning for both males and females and suggest a functional role for androgens in follicular maturation or ovulation.

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AULETTA, E. J., B. V. CALDWELL, and G. L. HAMILTON. 1974. Androgens: testosterone and dihydrotestosterone. *In* Methods of hormone radioimmunoassay. *Edited by* B. M. Jaffe and H. R. Behrman. Academic Press, New York. pp. 359–370.

BARGER, L. E., L. A. COLLINS, and J. H. FINUCANE. 1978. First record of bluefish larvae, *Pomatomus saltatrix*, in the Gulf of Mexico. Northeast Gulf Sci. **2**: 145–147.

BARR, A. J., J. H. GOODNIGHT, and J. P. SALL. 1979. SAS user's guide. SAS Institute Inc. Raleigh, North Carolina.

BEAUMARIAGE, D. S. 1973. Age, growth, and reproduction of king mackerel *Scomberomorus cavalla* in Florida. Fla. Mar. Res. Publ. **1**: 1–45.

BRACHET, J. 1978. The hormonal induction of maturation in amphibian oocytes. Med. Biol. **56**: 304–309.

CAMPBELL, C. M., and D. R. IDLER. 1976. Hormonal control of vitellogenesis in hypophysectomized winter flounder (*Pseudoplueronectes americanus* Walbaum). Gen. Comp. Endocrinol. **28**: 143–150.

CAMPBELL, C. M., J. M. WALSH, and D. R. IDLER. 1976. Steroids in the plasma of the winter flounder (*Pseudopleuronectes americanus* Walbaum). A seasonal study and investigation of steroid involvement in oocyte maturation. Gen. Comp. Endocrinol. **29**: 14–20.

CRIM, L. W., and D. R. IDLER. 1978. Plasma gonadotropins, estradiol, and vitellogenin and gonad phosvitin levels in relation to the seasonal reproductive cycles of female brown trout. Ann. Biol. Anim. Biochim. Biophys. **18**: 1001–1005.

DINDO, J. J., and R. MACGREGOR III. 1981. Annual cycle of serum gonadal steroids and serum lipids in striped mullet, *Mugil cephalus*. Trans. Am. Fish. Soc. **10**: 403–409.

ECKSTEIN, B., M. ABRAHAM, and Y. ZOHAR. 1978. Production of steroid hormones by male and female gonads of *Sparus aurata* (Teleostei, Sparidae). Comp. Biochem. Physiol. **60**(13): 93–97.

ECKSTEIN, G., and Y. KATZ. 1971. Steroidogenesis in post-and pre-spawned ovaries of a cichlid fish, *Tilapia aurea*. Comp. Biochem. Physiol. **38A**: 329–338.

FINUCANE, J. H., H. A. BRUSHER, and L. A. Collins. 1980. Spawning of bluefish, *Pomatomus saltator*, in the northeast Gulf of Mexico. Northeast Gulf Sci. **4**: 57–59.

FONTAINE, M. 1976. Hormones and the control of reproduction in aquaculture. J. Fish. Res. Board Can. **33**: 922–939.

IDLER, D. R., D. A. HORNE, and G. B. SANGALANG. 1971. Identification and qualification of the major androgens in testicular and peripheral plasma of Atlantic salmon (*Salmo salar*) during sexual maturation. Gen. Comp. Endocrinol. **16**: 257–267.

IWAMATSU, T. 1978. Studies on oocyte maturation of the madaka, *Oryzias latipes*. On the structure of steroids that induce maturation *in vitro*. J. Exp. Zool. **204**: 401–408.

JALABERT, B. 1976. *In vitro* oocyte maturation and ovulation in rainbow trout (*Salmo gairdneri*), northern pike (*Esox lucius*) and goldfish (*Carassius auratus*). J. Fish. Res. Board Can. **33**: 974–988.

KATZ, Y., and B. ECKSTEIN. 1974. Changes in steroid concentration in the blood of female *Tilapia aurea* (Teleostei, Cinchlidae) during initiation of spawning. Endocrinology, **95**: 963–967.

KENDALL, A. W., JR., and L. A. WALFORD. 1979. Sources and distribution of bluefish (*Pomatomus saltatrix*) larvae and juveniles off the east coast of the United States. Fish. Bull. U.S. **77**: 213–227.

LAMBERT, J. G. D., G. I. C. G. M. BOSMANN, R. VAN DEN HURK, and P. G. W. J. VAN ORDT. 1978. Annual cycle of plasma oestradiol-17β in the female trout *Salmo gairdneri*. Ann. Biol. Anim. Biochim. Biophys. **18**: 923–927.

LANCE, V., and I. P. CALLARD. 1978. Hormonal control of ovarian steroidogenesis in nonmammalian vertebrates. *In* The vertebrate ovary. *Edited by* R. E. Jones. Plenum Publ. Corp., New York. pp. 361–407.

ORCZYK, G. P., B. V. CALDWELL, and H. R. BEHRMAN. 1974. Estrogens: estradiol, estrone, and estriol. *In* Methods of hormone radioimmunoassay. *Edited by* B. M. Jaffe and H. R. Behrman. Academic Press, New York. pp. 333–345.

OZON, R. 1972. Androgens in fishes, amphibians, reptiles, and birds. *In* Steroids in nonmammalian vertebrates. *Edited by* D. R. Idler. Academic Press, New York. pp. 328–389.

SCHMIDT, P. J., and D. R. IDLER. 1962. Steroid hormones in the plasma of salmon at various stages of maturation. Gen. Comp. Endocrinol. **2**: 204–214.

SCHUETZ, A. W. 1974. Role of hormones in oocyte maturation. Biol. Reprod. **10**: 150–178.

TATA, J. R. 1978. Induction and regulation of vitellogenin synthesis by estrogen. *In* Biochemical actions of hormones. *Edited by* G. Litwack. Academic Press, New York. pp. 397–431.

WILK, S. J. 1977. Biological and fisheries data on bluefish, *Pomatomus saltatrix* (Linnaeus). Natl. Mar. Fish. Serv., NEFC, Sandy Hook Lab., Tech. Ser. Rep. **11**: 1–56.

WINGFIELD, J. C., and A. S. GRIMM. 1977. Seasonal changes in plasma cortisol, testosterone and oestradiol-17β in the plaice, *Pleuronectes platessa*. Gen. Comp. Endocrinol. **31**: 1–11.